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Population structure and persistence of Lahontan cutthroat trout: results from a comparative study of isolated and networked streams

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Population structure and persistence of Lahontan cutthroat trout: results from a comparative study of isolated and networked streams

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SUMMARY

We discuss evidence that Lahontan cutthroat trout (LCT) exhibit the potential to benefit from a networked population structure. We present analyses of recruitment and survival in isolated and networked populations in the northeastern portion of the species' range, and formulate models for projecting the dynamics of each population under hypothetical future environments. Environments considered include altered stream flow regimes, reduced habitat, increased harvest, or continuation of recent conditions. Our models predict that population risk is low under recent stream conditions in all streams, but that all isolated streams are at high risk under several of the hypothetical environments. Although subpopulations within the Marys River network are at high risk under most models, our results indicate that the networked population is more robust than the isolated populations. We present evidence that the persistence of the networked population results from a) individuals experiencing different environments at different locations, and b) individuals moving between different locations at sufficient rates to modulate population fluctuations that might otherwise lead to local extinction. These conditions favor metapopulation or source-sink dynamics that can boost persistence in systems suffering local perturbations. We discuss the general potential for metapopulation and source-sink dynamics in LCT, and make several general recommendations for LCT management.

INTRODUCTION

Population biologists have long recognized the potential for loosely networked populations to persist despite local catastrophes (Andrewartha & Birch 1954, Huffaker 1958, den Boer 1968). Provided that individuals at different locations experience different environments, and provided that individuals move between different locations at sufficient rates, environmentally-induced population fluctuations can be offset by exchange between adjacent populations.

In extreme cases, local catastrophes may cause local extinction. If these extinctions are offset by recolonization, we can describe the system as a metapopulation (Levins 1969), in which extinction and recolonization of local populations is similar to birth and death of individuals within a single population. In metapopulations, as in single populations, a fluctuating equilibrium can be reached in which losses are generally balanced by gains.

A similar mechanism of population modulation involves the movement of individuals from areas of population growth to areas of population decline, which can prevent local extinction while modulating local fluctuation. This modulation mechanism is often termed source-sink dynamics (Pulliam 1988). The status of a population as a source or sink may vary or reverse, depending on environmental conditions and population density (Watkinson & Sutherland 1995, Boughton in press).

In practice, it may be difficult to determine whether metapopulation or source-sink mechanisms (or some combination thereof) are responsible for population modulation. It may be difficult to detect brief local extinctions (Hanski 1998), or to determine which areas (if any) harbor permanent source populations (Dias 1996). In this report, we consider a broad definition of networked populations, encompassing metapopulation and source-sink systems. We address the potential for each mechanism to operate, alone or in combination, within a networked population of the threatened Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*). We compare the potential for persistence of this networked population to the potential for persistence of several isolated populations.

Specifically, we discuss evidence that Lahontan cutthroat trout (LCT) exhibit the potential to benefit from a loosely networked population structure. We analyze and model the dynamics of isolated and networked populations, and compare persistence predictions under hypothetical future environments. Our preliminary analysis of one stream network indicates that a) individuals at different locations in the network experience different environments, and b) individuals move between different locations at sufficient rates to modulate population fluctuations that might otherwise lead to local extinction. Our results indicate that the networked population is more robust than the isolated populations to some potential environmental threats. In light of these results, we make several general recommendations for LCT management.

BACKGROUND

Study populations

This analysis is based on six streams in the northeastern Lahontan Basin. Three of these streams (Gance Cr., Frazier Cr. and Foreman Cr.) are isolated, rarely or never flowing into a mainstem. Three form part of a stream network within the Marys River Basin (East Marys R., West Marys R. and Marys River Basin Cr., abbreviated below as EMR, WMR and MRBC). Each stream contains Lahontan cutthroat trout (LCT) and few non-native fish. The streams are roughly similar in average width (range 1.6-3.1 m), average depth (range 10-16 cm), average elevation (range 1975-2670 m) and stream flow patterns ($R^2 = 0.79$ for average daily flows in Gance Cr. and Marys R. over the period 1979-1987). We also estimate that average population sizes over the years 1993-1999 were roughly similar between streams (range 1067-2765, excluding young-of-year). (Data above are from Dunham 1996, Dunham et al. 1997, Dunham et al. 1999 and Ray et al. in prep.)

Data

Population data

Age-structured demographic data were collected from each stream population for the years 1993-1999 by researchers at the University of Nevada, Reno. Comparable data were collected from Gance Cr. for the years 1979-1985 by Platts and Nelson (1988). All data are estimates of yearly age class size, based on electrofishing in several block-netted portions of each stream during lowest flows in August. In each sample reach, three or more passes of electrofishing were employed in order to deplete the reach of fish. Captured fish were held until sampling was completed, then measured and returned

to the stream. Earlier samples (Platts & Nelson 1988) were taken from three reaches per stream (total = 549m sampled), and later samples (Dunham 1996, Dunham & Vinyard 1997) were taken from seven to 15 reaches per stream (total = 175-375m sampled).

Estimates of the true population size within each sampled reach were obtained using Microfish software (Van Deventer & Platts 1985), which computes the number of uncaptured fish by extrapolating from the decline in fish capture with each repeated pass of electrofishing. Total population estimates for each stream were determined by combining sample reach population estimates and multiplying by the ratio of total occupied stream length to sampled stream length. Total occupied stream length was determined by exhaustive sampling conducted in 1997 (Dunham et al. 1999). MIX software (MacDonald & Pitcher 1979) was used to translate the size distribution of all sampled fish into age class proportions for each stream and year. The MIX analysis was seeded with estimates of age/size relationships determined from otolith data (Ray et al. in prep.; see Kruse et al. 1997 for use of otoliths in aging cutthroat trout). Otoliths were obtained from LCT captured in Gance Cr. Age class sizes for each stream and year were estimated as the age class proportions determined by MIX analysis, multiplied by the total population estimate described above.

Stream flow data

We use data on stream discharge to characterize recruitment in several streams (see below). Data on average daily discharge are available from the USGS for the Marys R. for the years 1943-1999 from a metering station below the confluence of EMR, WMR and MRBC. Similar data are available for Gance Cr. for the years 1979-1987. Although these two metering stations are located in different drainages and are separated by at least 100 km, correlation between flows is high (R^2 = 0.86 for $\log_{10}$-transformed daily flow data from 1979-1987; R^2 = 0.79 for "Spring" flows only [see below]). This result implies high correlation in stream flows across the northeastern Lahontan Basin. Therefore, we use the lengthy data set on flows in the Marys R. to characterize long-term flow variability in all streams modeled here.

Model development

Overview

We use data on age-structured population size and stream flow to develop simple linear models of LCT recruitment and survival in each stream or stream network. Recruitment is a linear function of the number of reproductive adults and/or certain stream flow variables. Class survival is a linear function of class density.

The dynamics of isolated populations (Gance, Frazier and Foreman) are modeled with a single recruitment model and one survival model per age class. The dynamics of populations within the Marys River network are modeled in three different ways. First, we assume all age classes move freely between the tributaries. For this *pooled* model, we pool the data from WMR, MRBC and EMR to develop a single recruitment model and one survival model per age class, so dynamics can be modeled as if this were one population. Second, we assume that WMR, MRBC and EMR populations are completely isolated, and we develop separate recruitment and survival models for each stream. Third, we assume limited movement of fish between streams. For this *networked* model, we analyze local recruitment and survival with respect to local densities and densities in

other parts of the stream network. If local recruitment is a function of the number of adults in the entire network, movement of adults is implicit in the model. If local survival of an age class is a function of class density in another part of the network, movement of the class is implicit in the model. Using this approach, we can model the movement of each age class between streams *implicitly*. This approach generates separate recruitment models for each population and separate survival models for each class within the network.

Using the linear recruitment and survival models developed for a single population or a population network, we project growth under hypothetical future environments. All projections are based on simulations that incorporate observed variance in demographic rates and stream flow rates. Because we do not estimate other aspects of uncertainty in these data, our models may underestimate the *absolute* variance in population numbers. However, this preliminary analysis should provide reliable estimates of the *relative* risk of networked versus isolated populations. These issues are addressed further below. Here, we present our approach for developing recruitment, survival and simulation models, the details of our hypothetical future environments, and our criteria for population persistence.

Recruitment models

Poor relationship between adults (t) and YOY (t)

Recruitment can be defined as the number of juveniles entering the population in late summer, which is a function of the number of reproductive individuals spawning in early summer and the survival of eggs and YOY through late summer. In this study, streams were sampled annually in August, so we expected the number of YOY in August to be related to the number of reproductive adults (age 3+ and older) present in concurrent samples. In practice, we found little relationship between YOY and adults in these populations. We suspect that our samples of YOY do not represent of the true number of YOY in the stream, for two reasons. First, the timing of YOY emergence corresponds closely with the sampling period, as both occur during lower stream flows. As a result, variability in the timing of emergence contributes to unexplained variance in YOY estimates. Second, due to their relatively low mobility and initial association with spawning gravels, the spatial distribution of YOY is less uniform than other classes, especially if they emerge from gravels shortly before sampling takes place. Therefore, when our samples do not include a representative density of spawning gravels, poor estimates of YOY density may ensue. Improving these estimates would require a separate estimate of the density of spawning gravels in the entire habitat, relative to the sampled reaches. In this study, the number, location and quality of spawning gravels shifts yearly in response to Spring stream flows, so rapid assessment of these gravels is infeasible.

Limited relationships between adults and recruitment

Recruitment can also be defined as the number of Class 1 fish (age 1+) entering the population. Class 1 fish censused in year t were produced by reproductive adults (age >=3+) in year t-1. We found evidence for a relationship between Class 1 (t) and adults (t-1) only in Foreman Cr., WMR and MRBC (Table 1). We found no evidence for negative effects of adults in year t on recruitment in year t or t+1 (e.g., cannibalism or cross-class density-dependence).

Widespread relationships between stream flow and recruitment

Recruitment may also be influenced by stream flow (Nehring & Anderson 1993, Latterell et al. 1998). Most of the variance in stream discharge in this region occurs during the "Spring" (March 1 through June 30). The standard deviation of average daily discharge (in cubic feet per second) is 154 in the Spring (n = 6710) and just 35 at other times of year (n = 13136). We hypothesize that high Spring flows may benefit spawning activity and egg survival, while reducing the survival of pre-Class 1 fish. We find support for these hypotheses in the long LCT data set from Gance Cr. Recruitment of class 1 fish in the fall of year t is positively related to average daily flows in the Spring of year t-1 ($P = 0.02$, $R^2 = 0.34$) and negatively related to average daily flows in the Spring of year t ($P = 0.09$, $R^2 = 0.20$). A multiple linear regression of recruitment on both flow variables is highly significant ($P = 0.002$) and explains 64% of the variance in recruitment in the Gance population (Fig. 1). Similar relationships between recruitment and Spring discharge are found within most populations (Table 1). Other flow variables that might predict recruitment (e.g., maximum discharge, or frequency of high discharge) are not particularly explanatory in this study. Other trout studies also identify average discharge as the most explanatory flow variable affecting recruitment (Latterell et al. 1998).

Data transformation

The only independent variables tested as recruitment predictors were the number of reproductive adults and the stream flow variables. These data were subject to various transformations intended to normalize model residuals, in preparation for simulating the unexplained variance according to a normal distribution. There is little effect of data transformation on the distribution of residuals in these models (Fig. 2). We use untransformed class size data and $\log_{10}$-transformed flow data in all recruitment models (Fig. 2b).

Model selection

Model selection is influenced by the fact that data from all years are not of equal quality. In 1993 and 1999, sample sizes from the Marys River were much lower than in 1994-98.

year	1993	1994	1995	1996	1997	1998	1999
n	33	123	95	83	98	123	44

In 1993, age structure could not be determined for fish in MRBC, due to small sample size (n = 6 fish larger than YOY). Lacking data from MRBC, we can not use 1993 data for either the pooled or networked Marys River models. Although MIX analyses indicate high confidence in age structure estimates for WMR and EMR in 1993, and for all three tributaries in 1999, we avoid data from these years where possible. Table 1 shows correlation coefficients for models developed with and without data from 1993 and 1999. In general, recruitment is explained best by data from 1994-98, although most models retain explanatory power when 1993 and/or 1999 data are included.

Analyses reveal only one explanatory recruitment model for each of the isolated streams and one for the pooled population in the Marys River tributaries (Table 1). Models for isolated streams tend to be highly significant. In the Marys River populations, recruitment

models tend to be less explanatory and lack significance, perhaps due to the shorter time-series of useful data. For WMR and MRBC, several models are explanatory but not significant. Rather than select the "best" model, we compare the results of simulations based on four different recruitment models for each of these streams. In EMR, no model is particularly explanatory. In fact, the only model that explains any variance (model EMR_1, Table 1) relates recruits in year t *negatively* with flow in the previous year and *positively* with flow in the current year, in opposition to other recruitment models. One possible explanation for this non-intuitive model is habitat selection by adults and recruits. If fish can choose freely between Marys River tributaries, and if flows are *relatively* lower in EMR due to some quality of the drainage or stream channel, then in high-flow years adults may leave EMR to spawn, while recruits move in to seek relative shelter. We avoid further speculation and simply compare results based on this model with those based on a model in which recruitment is predicted by its observed mean and standard deviation (model EMR_2, Table 1).

Combining local recruitment models in the *networked* Marys River model

If adults could move freely among the Marys River tributaries, and if adults were an important predictor of recruitment, we would expect local recruitment to be a function of the number of adults in the entire network. The only evidence for this model appears in the 1994-98 data from WMR (model WMR_4, Table 1). More commonly, local recruitment is related to local adults and stream flow, as in isolated populations. Each tributary exhibits a different potential for recruitment in the same year, due to different independent variables affecting recruitment or different regression parameters. This potential for distinct recruit densities in each tributary makes the networked model more realistic and powerful than the pooled Marys River model.

Among the three tributaries there are 10 potential recruitment models (WMR_{1-4}, $MRBC_{1-4}$ and EMR_{1-2}). Some of these (WMR_{1-3} and EMR_{1-2}) can be used to project the dynamics of tributary populations in isolation, because they do not require immigration of adults to complete reproduction. All can be used in the networked model, because network model assumptions allow for local or global movement of adults. Using each unique combination of these 10 models, we create 32 unique versions of the networked Marys River model. All versions of the network recruitment model share one version of the network survival model, described below and in Table 3.

Survival models

We find consistent, negative relationships between survival and density within classes, especially in the younger classes (Table 2). These relationships tend to be significant, even in the smaller data sets from the Marys River tributaries. In the large data set from Gance Cr., significant density-dependence is found in all the younger (and more populous) age classes. Lagged density-dependence is marginally significant for one age class in Gance Cr.: Class 2 survival depends on the density of Class 1 in the previous year. No other lagged or cross-class density-dependence was identified.

Data transformation

Survival is estimated as the number in Class X in year t divided by the number in Class X-1 in year t-1. In order to normalize residuals in a linear model, survival rates are ln-

transformed, which requires adding a small number (0.01) to avoid ln(0). Density is estimated as the (untransformed) number of individuals estimated to be in the class.

Evidence for movement of fish among tributaries of the Marys River

Class 3 fish almost certainly move between tributaries of the Marys River (Fig. 3). We observe a consistent excess of Class 3 in WMR, and a consistent deficit of Class 3 in MRBC. In most years, there are more Class 3 individuals in WMR in year t than there were Class 2 individuals in the previous year. In all years, there are zero Class 3 individuals in MRBC, but some Class 4 individuals. This pattern is consistent with the movement of (pre-census) Class 3 individuals from MRBC to WMR and the return of surviving (pre-census) Class 4 individuals from WMR to MRBC. However, there are many more complex patterns of movement that are consistent with this same pattern.

We find more evidence for movement when we examine relationships between survival within the local stream and density within other streams or the entire stream network (Table 3). Note that the majority of intercepts in these regression models are positive, which translates into "survival" > 1 for populations at low density. This pattern implies that most populations and classes can receive immigrants at some time, so movement is likely. These positive intercepts do not translate into high immigration at low network densities. Instead, network densities rarely fall, due to the potential for constant, density-dependent movement, described below.

Evidence for movement between specific streams is easy to find. Beginning with Class 1, movement between MRBC and EMR is suggested by a significant, negative relationship between survival of Class 1 in MRBC and density of Class 1 in both MRBC and EMR. Correlation between local survival and density in a different stream could be due to correlated densities among streams. But in this case, Class 1 densities appear to fluctuate independently in MRBC and EMR ($R^2 = -0.46$). A similar pattern is seen for Class 2 in EMR, where local survival again depends on density in both MRBC and EMR. In this case, class densities fluctuate in near opposition in the two streams ($R^2 = -0.76$), so correlated density is out of the question.

The potential complexity of movement within this network is indicated by returning to the problem of excess Class 3 fish in WMR (Fig. 3). Invoking the simplest explanation for the patterns observed in Fig. 3, Class 2 "survival" in WMR should depend on Class 2 density in MRBC. Instead, Class 2 "survival" in WMR depends on Class 2 density in EMR. However, Class 2 "survival" in EMR depends on Class 2 density in MRBC, providing a mechanism for density in MRBC to affect density in WMR! The simplest (probably simplistic) interpretation of these relationships involves fish from MRBC attempting to move first into EMR and second (if densities in EMR are high) into WMR.

Combining movement and survival in models for the Marys River network

In an isolated population, class survival rates can be estimated from a time-series of class size data, and these rates will generally be less than one (although sampling error may cause frequent over- and underestimates). In a networked population, class "survival" includes immigration and emigration. Although immigration is implied when survival rates exceed one, immigration can also raise survival rates to values that remain less than one. The immigration hidden in "survival" data can be used to model movement and network dynamics *if* relationships between "survival" and density are

determined at appropriate spatial scales. With the data from the Marys River tributaries, we can explore relationships between "survival" and density at three scales (within a stream, across two streams and across the entire network). Ideally, the model predicting "survival" with best fit will be the one in which the independent variable (density) is determined at the scale of significant population mixing. By simply using this best-fit model, we can theoretically mimic the natural scale of density effects on survival and the transfer of individuals.

Unfortunately, by searching for the best model at a range of scales, we increase the probability of finding a model with spuriously good fit. We searched through seven models per class to find the location and scale most responsible for survival and movement (local stream x, stream y, stream z, stream x+y, stream x+z, stream y+z and stream x+y+z). The models in Table 3 have suspiciously good fits for short data sets. However, our experience in analyzing the data was that only one or two models per class tended to have any explanatory power, and those had very high R^2. There was little opportunity for choosing one model that was incrementally better than others due to some statistical coincidence.

Nevertheless, we note that the behavior of the network model was somewhat unrealistic when only these best-fit models were employed to predict class survival+movement. In particular, some of the older age classes would occasionally "spike" to high numbers. In order to maintain realistic dynamics, we use the survival+movement models to obtain the *relative* survival of age classes in different streams (i.e., to partition surviving individuals among streams), and we use the survival model for the pooled Marys River (Table 2) to control the *absolute* rate of survival across the entire network. This model produces dynamics strikingly similar to those observed in the Marys River data, as discussed below.

Population projection models

Combining recruitment and survival models, we project population growth into the future using stochastic simulation models. Each simulation begins with the population at its current size and age class distribution. Next, 100 years of stream flow are drawn at random with replacement from the 55-year time series of data available for the Marys River. (Flows are sampled at random because there is no detectable trend or autocorrelation in this time series.) Next, the current number of reproductive adults is assessed. If the number is greater than some threshold, then reproduction occurs. For the results shown in Table 4, the threshold was 20 adults. If the number of adults falls below the threshold, recruitment fails whether or not recruitment is a function of adult numbers. Within the Marys River network, local recruitment fails if 20 reproductive adults are not available locally, whether or not local recruitment is a function of local adults. For each population in the model, a recruitment value is predicted using the recruitment model (Table 1) plus an error patterned on the distribution of recruitment model residuals (assuming a normal distribution with standard deviation given in Table 1). Next, the survival or survival+movement of individuals is predicted for each class using the models in Table 2 or 3 (including error patterned on the distribution of survival model residuals). Finally, the population or network is tested for being "at risk", which is defined here as fewer than 50 individuals, including fewer than 20 adults. If the population or network is not at risk, the simulation continues for 100 time steps (100 years). Each population or network model is simulated 500 times to determine the probability of risk within the next 100 years.

Simulation of altered environments

The population projections described above assume that the current environment will remain relatively unchanged over the next 100 years. However, because our recruitment models incorporate environmental variability (stream flow) and our survival models incorporate effects of population density, we can also project population dynamics under assumptions that the environment will change in several ways. We apply 10 different treatments to the "base model," the recruitment and survival models in Tables 1-3.

1. *Higher variance in recruitment.* We multiply the standard deviation of the recruitment model by a factor of 1.5. In the base models, we assume no sampling error in our data. Exploring the effects of increased error is one way to determine how robust are model results to this assumption. This treatment also models the effect on persistence of elevated environmental stochasticity in recruitment.
2. *Higher variance in survival.* We multiply the standard deviation of the survival model for each class by a factor of 1.5, for reasons similar to those in 1.
3. *Higher variance in recruitment and survival.* We multiply the standard deviation of the recruitment and survival models by a factor of 1.5, for reasons similar to those in 1.
4. *Truncated survival.* We do not allow survival >1. Because survival rates > 1 in isolated populations may be erroneous, this treatment provides a more conservative estimate of viability. On the other hand, allowing for sampling error, we would expect as many underestimates of survival as overestimates. (This may not be true if there were bias in our sampling, such that the fraction sampled declines with density; we have searched for this type of error and have found no effects of density in fraction sampled. Ray et al. in prep.) Therefore, truncating survival at 1 should bias survival rates downward unrealistically. Truncating survival also reduces the potential for immigration, although immigration can occur without causing survival rates to exceed 1. Even with survival rates < 1, the Marys River network still operates as a population network, including some effects of movement between classes in different populations.
5. *Higher stream flow.* We multiply stream flows by a factor of 2, which also increases the variance in flow. This treatment may mimic changes in stream discharge within the Lahontan Basin predicted by certain models of global climate change.
6. *Lower stream flow.* We multiply stream flows by a factor of 0.5, which also reduces the variance in flow. This treatment may mimic changes in stream discharge within the Lahontan Basin predicted by the other guy's models of global climate change, or certain dewatering strategies.
7. *Lower stream capacity for recruitment.* We reduce the intercept of the recruitment model, to mimic the potential effect of reducing the number of spawning gravels in the stream. All populations except Foreman have a positive intercept in the recruitment model. For these models, the intercept is halved. In the Foreman model, the negative intercept is doubled.
8. *Lower capacity for adults.* We increase the slope of the survival model, to mimic the loss of adult habitat within the stream. Negative coefficients of regression are multiplied by 2, in an attempt to halve adult carrying capacity. (The models have no set carrying capacity, but a capacity is reached due to density-dependent survival in one or more age classes.) Coefficients of zero (e.g., S_4 in Gance Cr.) are not altered, because there is no evidence for density-dependence in these classes. Due to this latter assumption, this model probably underestimates the effect of halving the stream capacity.

9. *Lower stream capacity.* We apply treatments 7 and 8 in tandem. This treatment may provide a reasonable facsimile for the effect of losing half the habitable stream reach.
10. *10% harvest.* We harvest exactly 10% of Class 1 in each year in which the class exceeds 500 fish. This treatment is designed to test the effect of removing young fish for transplants or hatchery purposes. Normally, a large portion of the fish removed for these purposes might be YOY. We cannot include YOY in most of our models, for reasons described above (see "Recruitment models"). Our harvest model may overestimate the impact of removing 10% of YOY, because a larger percentage of YOY are probably lost to mortality between years than the percentage of Class 1 that is lost between years. However, because it is extremely difficult to estimate the size of the YOY class, it is possible that much more than 10% would be taken, even when 10% is the target harvest. Therefore, we are uncertain about how this treatment relates to the impact of harvesting YOY. We include it here for comparison with the effects of other potential impacts on these populations.

RESULTS

"Base model" results

None of the "base models" (in Tables 1-3) predict that population sizes will decline from those observed over the past few years (Table 4, Figs. 4 and 5). All populations are predicted to maintain roughly similar sizes over the next 100 years, provided stream flows follow the same distribution as observed over the past 55 years, and provided the factors affecting recruitment and survival in each class remain unchanged. The general agreement between model predictions and recently observed population and class sizes increases our confidence in the use of the less significant models in Tables 1-3.

Unlike the results of a simple Leslie matrix model of population growth, these models do not predict a trend in abundance. Due to density-dependent survival in one or more age classes, these models predict a long-range population growth rate (lambda) near one, and a quasi-equilibrial population size. Extinction can still occur due to environmental stochasticity (modeled as the variance in recruitment and survival) or due to an interaction between environmental stochasticity and the natural population cycles induced by the age structure in these models.

What is remarkable about these models is that they predict quasi-equilibrial sizes of populations and classes that are very similar to the sizes recently observed. These observed average population and class sizes were not explicitly used in fitting the recruitment and survival models. The fact that predictions match observations so closely may indicate that the recruitment and survival models used are good representations of realized recruitment and survival relations in wild trout.

Figure 4 shows the relationship between recently observed population and class sizes and long-range projections based on our models for isolated populations and the *pooled* Marys River population. Note that our models predict somewhat larger average numbers in the older age classes in several of these models. We believe these projections may be overestimates, due an artifact of our approach to modeling variance in survival rates. We assume a normal distribution of residuals, which appears to be reasonable in the younger age classes. We have more data for these younger age classes, so we use these data to guide our model selection. However, the distribution of residuals may not

be normal for the older age classes. Perhaps fewer high survival rates are observed than lower rates (we have insufficient data to test this hypothesis). Even if residuals are normally distributed, the large standard deviation of these residuals in the older age classes (see Table 2) will bias our estimates of survival upward for these classes. This bias occurs because no values lower than zero can be chosen for survival, but very large values can sometimes be chosen. We do not believe that this potential artifact biases our conclusions about the relative persistence of isolated versus networked populations. We use similar residual models for both isolated and networked populations, so our comparative study should be robust. Furthermore, recruitment is rarely a function of adult density, so the survival of a few more adults in the older classes should not have a large effect on population dynamics. In the one model most influenced by adult reproduction, the Foreman Cr. model, we do not observe this potential artifact in the results (Fig. 4).

Figure 5 shows results from four of the 32 models used to project the networked dynamics of the Marys River population. The main point of this graph is that all four models are in very good agreement about the future size of this network. These four models are responsible for over 74% of the variance in results of the 32 network models, yet their predictions are quite similar. This graph addresses the similarity in *average* predicted and average observed population data. Predictions and observed data also correspond in their extreme values. If observed averages and extrema are plotted against predicted averages and 95% confidence bounds for every class size in the network, $R^2 > 0.95$, $0.95<m<1.7$, and $4<b<28$ for all 32 models.

The very positive intercepts on most of the Marys River survival+movement models do not appear to result in massive exchange between populations. Local populations go extinct with high frequency (not shown). Network densities generally remain high enough that survival rates are bounded below one.

Response to alternative model treatments

The most striking result from this modeling exercise is the relative robustness of the Marys River network. Regardless of the model employed, we predict that this population or network is at very low risk, despite being comprised of apparently high-risk subpopulations (Table 4). In all of the 32 network models, at least one of the Marys River tributary populations is predicted to be at highest risk (1.0). The only treatment that presents even minimal risk to the Marys River network in these models is truncated survival, which reduces survival and the potential for density-dependent redistribution of fish between streams. The highest risk predicted for this population is 0.02, while the highest risk predicted for other populations ranges from 0.49 to 1.0.

Although these models do not account for all critical sources of variance in population size (e.g., sampling error), they are likely sufficient for predicting the *relative* persistence of isolated versus networked populations. Clearly, this networked population is more robust, whether all individuals move freely between streams (pooled model) or whether dynamics are spatially structured (networked model). In fact, under one of the treatments (lower capacity), all three isolated populations develop unacceptable levels of risk, while the Marys River network maintains zero risk.

The treatment with most dramatic effect on population risk is lowered stream capacity This is the only treatment that significantly enhances risk under the Gance population

model. The Gance model is probably affected by reduced capacity due to the tight density-dependence in most age classes. Under the Frazier population model, reduced recruitment capacity and higher stream flows both put the population at highest risk, due to the solely negative effect of flow on recruitment in this model (Table 1). The Foreman model suffers under higher variance in survival rates, which are normally low. Three treatments that have very minor effects across model populations are higher variance in recruitment, lower stream flows and our model of 10% harvest in Class 1.

DISCUSSION

Across all models and treatments, three important patterns emerge (Table 4). First, the isolated populations exhibit some degree of vulnerability to current or foreseeable conditions. Second, subpopulations in the Marys River exhibit substantial vulnerability under most models. Third, the Marys River network as a whole is robust. These results depend on the relative potential under different models for population response to a changing environment (in this case, changing stream flows and class densities).

In our models of isolated or spatially restricted populations, there are a limited number of ways to respond to density (namely, the 4 or 5 survival models for each class), and individuals within a class must respond in a fairly uniform manner to each new density environment (i.e., they must respond to the survival model for their class). These individuals have few options, and their populations have few trajectories to use in circumventing environmental insults. In our models of networked populations, each subpopulation may respond to changing densities in a different way, so the fate of an entire age class is not altered in the same way by the environment. In this sense, our networked model captures the important elements of metapopulations and source-sink dynamics.

In reality, we don't know *a priori* whether there is less potential for semi-independent network dynamics in Gance Cr. than in the Marys River headwaters. We must infer this information from the demographic data. Several simple observations illustrate the relative potential for independence between individuals in the two systems. The first set of observations focuses on survival+movement relationships. The second focuses on recruitment.

First, the potential for any sort of metapopulation or source-sink dynamics depends on the movement of individuals between semi-independent populations. There is evidence for movement but no evidence for independence in the Gance data. Strong density-dependence within Class 1 in Gance Cr. indicates that these fish experience and respond to similar environments as a unified class. In contrast, there are several lines of evidence pointing to semi-independent dynamics in the Marys River data. We know that there is strong density-dependence in Classes 2 and 3 in the pooled Marys River data. This result indicates that there must be density-dependence in Class 1, which is much more numerous. The fact that no density-dependence is seen in the pooled data indicates that Class 1 experiences densities on a spatial scale smaller than that of the network (Ray & Hastings 1996). Not surprisingly, Class 1 exhibits density effects at the level of one or two streams within the network (Table 3). These observations imply semi-independent population dynamics within the network, mediated by imperfect mixing of Class 1. We also have evidence from demographic data that Class 3 is imperfectly distributed in the network (Fig. 3). Examination of survival relationships between classes

and streams (Table 3) suggests that after age 2, fish move from one stream to another until most of them end up in WMR at age 3. Finally, if we look for correlation in class sizes across years, we find that class sizes in WMR and MRBC are somewhat correlated (R^2 = .71), but classes MBRC and EMR are uncorrelated (R^2 = -.02) and classes in EMR and WMR are negatively correlated (R^2 = -.32). All of these observations suggest mechanisms for limited movement that could facilitate persistence through metapopulation dynamics or source-sink mechanisms.

Second, there may be important differences in local environmental variables that convey some independence between individuals in different portions of the Marys River network. For example, each stream population exhibits a very different relationship between adults, flow and recruitment. Not only do the independent variables differ between populations, but even the sign of coefficients can be reversed (model EMR_1, Table 1). The existence of several distinct but explanatory models for recruitment within one network certainly suggests the potential for semi-independent dynamics among network populations.

RECOMMENDATIONS

- We do not recommend managing the Marys River population network as if it were a metapopulation or a source-sink system. These terms are both broad and restrictive, in that they imply very general dynamics that may bear little resemblance to the demography in this network. Metapopulation dynamics imply complete local extinction and recolonization. Although we do see local extinction in our models of this network, these resemble spatial population shifts more than extinction. Recolonization occurs on a very short timescale, and whole classes may shift between streams in dynamics that are not addressed in any current "metapopulation" model. Similarly, although certain streams act as sources and others as sinks, the designation of source and sink changes rapidly with local densities. All streams contribute almost equally to recruitment over time, so none can be seen as "the" source population. A more fruitful approach might be to manage for diversity in habitats and independence among individuals, which generally means management that will prevent habitat degradation and simplification.

- Stream flow is an important variable determining at least some aspects of recruitment in this species. We could have developed better models for these populations if we had data on stream flow from a location within each population's distribution. Unfortunately, our stream flow data from the Marys River is obtained from below the confluence of WMR, MRBC and EMR. If we had more localized data, we could evaluate the importance of different recruitment relationships in EMR and other streams. These stream flow data could prove invaluable for predicting appropriate future habitats for the reintroduction of LCT. We recommend the placement of flow meters in potential reintroduction locations, and monitoring of flow variables during the early stages of reintroduction. This strategy may also be useful for monitoring environmental stochasticity in populations currently under threat.

- Our analyses indicate that there may be enough structural heterogeneity in the Marys River headwaters to maintain semi-independent dynamics among populations in tributary streams. We suggest that one criterion for selecting locations for

reintroduction or habitat restoration be some geographic measure(s) that would indicate whether the location exhibits a complexity on the order of the Marys River network. Measures could include stream orders and length of stream habitat, stream branching structure, variability in watershed aspects and slopes, types of vegetative cover, variability in streambed substrate size, etc. When planning for management of semi-independent populations, the key is variability in environment and limited (but significant) potential for movement. A complex environment will aid these goals.

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Table 1. Models for recruitment of Class 1 fish (age 1+) into each population or population network. R_t is the number of recruits in year t, predicted by stream flow and/or the number of reproductive adults in the previous year. Models shown for Gance, Frazier and Foreman are based on all available years of data, while models shown for Marys River populations are based on data from 1994-1998 (when sample sizes were large, allowing high confidence in age-structured class size estimates). Correlation coefficients in bold correspond to the models shown, while the additional column of correlation coefficients corresponds to similar regressions using all available years of data for the stream (both models are shown for WMR, because both are used in simulation models). The different models for Marys River recruitment assume (**a**) all classes move freely between tributaries, (**b**) populations in each tributary are isolated, or (**c**) adults move freely between tributaries. Note that the Gance recruitment model shown here is not as explanatory as the model based on Gance stream flows (Fig. 1). Here we project Gance recruitment using Marys River flows, because the short series of flow data from Gance Creek is insufficient for long-term projections. Note also that we project recruitment in each Marys River tributary under alternative models. Recruitment models shown for isolated streams are used in both single-population and networked population models. (See text for description of networked population models.) Finally, note that no recruitment model is possible for MRBC in isolation, because no Class 3 fish have been observed there (therefore, reproduction requires immigration of older fish).

Population	Recruitment model	SD_{resid}	P-value	$R^2_{94\text{-}98}$	$R^2_{All\ data}$
Gance Creek	$R_t = 1872\ flow_{t-1} - 2119\ flow_t + 2378$	770	0.022	**0.54**	
Frazier Creek	$R_t = -5029\ flow_t + 12617$	536	0.004	**0.83**	
Foreman Creek	$R_t = 1.85\ adults_{t-1} - 116$	178	0.001	**0.95**	
Marys River *pooled* (**a**)	$R_t = 609\ flow_{t-1} - 850\ flow_t + 2035$	290	0.465	**0.54**	0.17
Marys River *isolates* (**b**)					
WMR_1	$R_t = 1.76\ local\ adults_{t-1} - 4958\ flow_t + 10826$	94	0.402	**0.84**	0.67
WMR_2	$R_t = 0.78\ local\ adults_{t-1} - 1068\ flow_t + 2410$	150	0.315	0.84	**0.67**
WMR_3	$R_t = 484\ flow_{t-1} - 216\ flow_t - 165$	192	0.520	**0.48**	0.44
EMR_1	$R_t = -389\ flow_{t-1} + 535\ flow_t + 249$	253	0.623	**0.38**	0.33
EMR_2	$R_t = 441$	328	-	-	-
Marys River *networked* (**c**)					
WMR_4	$R_t = 1.83\ pooled\ adults_{t-1} - 7272\ flow_t + 15743$	108	0.380	**0.86**	0.00
$MRBC_1$	$R_t = 1.56\ local\ adults_{t-1} + 227$	85	0.219	**0.61**	0.63
$MRBC_2$	$R_t = -1262\ flow_t + 3290$	179	0.046	**0.78**	0.71
$MRBC_3$	$R_t = 3.11\ local\ adults_{t-1} - 1455\ flow_t + 3426$	35	0.259	**0.93**	0.68
$MRBC_4$	$R_t = 514\ flow_{t-1} - 1168\ flow_t + 1952$	104	0.074	**0.93**	0.81

Table 2. Models for survival of each age class, assuming each population is isolated. Models shown for Gance, Frazier and Foreman are based on all available years of data, while models shown for Marys River populations are based on data from 1994-1998 (when sample sizes were large, allowing high confidence in age-structured class size estimates). S_x is the natural log of survival ($\ln[n_{(x+1)t+1}/n_{(x)t}]+.01$) of individuals in Class x and $n_{(x)t}$ is the number of individuals in Class x in year t (the year is not designated in the table below). Correlation coefficients are as in Table 1. Note that the number of age classes surviving in each stream differs. For example, fish older than age 5 are not found within Gance Creek, so no survival model is needed past age 4. In MRBC, no Class 3 fish are observed, so this population cannot be modeled in isolation. In EMR, Class 4 fish are observed only in years following an absence of Class 3 fish. Therefore, we must assume zero survival of Class 3 in EMR, and immigration of older age classes (see the network model in Table 3). Finally, note that we accept density-dependent survival models whenever they explain over 40% of the variance in survival, regardless of model significance. Because density-dependent survival tends to increase the chance of persistence, using these models allows a more conservative assessment of whether isolated populations persist as well as networked populations.

Population	Class	Survival model	SD_{resid}	P-value	$R^2_{94\text{-}98}$	$R^2_{All\ data}$
Gance Creek	1	$S_1 = -0.0053\ n_1 - 0.2279$	0.6156	0.012	**0.48**	
	2	$S_2 = -0.0020\ n_2 + 1.1005$	0.7527	0.013	**0.48**	
	3	$S_3 = -0.0017\ n_3 - 0.5809$	0.7580	0.010	**0.50**	
	4	$S_4 = -2.2163$	1.8304	-	-	
Frazier Creek	1	$S_1 = -0.0004\ n_1 + 0.2702$	0.3312	0.025	**0.75**	
	2	$S_2 = -0.7270$	0.5842	-	-	
	3	$S_3 = -1.0567$	0.8530	-	-	
	4	$S_4 = -2.5154$	1.8375	-	-	
Foreman Creek	1	$S_1 = -0.0007\ n_1 - 0.0590$	0.7289	0.156	**0.43**	
	2	$S_2 = -0.2479$	0.3634	-	-	
	3	$S_3 = -0.0019\ n_3 + 0.1635$	0.4325	0.020	**0.74**	
	4	$S_4 = -2.9256$	1.9599	-	-	
	5	$S_5 = -0.3297$	0.3007	-	-	
Marys River *pooled*	1	$S_1 = -0.5936$	0.4364	-	-	-
	2	$S_2 = -0.0013\ n_2 + 0.5882$	0.0714	0.007	**0.99**	0.39
	3	$S_3 = -0.0046\ n_3 + 1.2678$	0.1697	0.026	**0.95**	0.64
	4	$S_4 = -0.2070$	0.5725	-	-	-
	5	$S_5 = -0.6913$	0.8608	-	-	-
WMR	1	$S_1 = -0.0056\ n_1 + 1.2799$	0.5056	0.061	**0.88**	0.87
	2	$S_2 = -0.0092\ n_2 + 2.2992$	0.2291	0.050	**0.90**	0.73
	3	$S_3 = -0.0020\ n_3 - 0.1139$	0.1611	0.111	**0.79**	0.79
	4	$S_4 = -0.0100\ n_4 + 1.6667$	0.4667	0.511	**0.48**	0.40
	5	$S_5 = -0.0084\ n_5 + 0.8655$	0.6735	0.256	**0.57**	0.52
EMR	1	$S_1 = -0.0039\ n_1 + 1.7409$	0.3397	0.043	**0.92**	0.86
	2	$S_2 = -0.0077\ n_2 + 1.2472$	1.5372	0.275	**0.53**	0.51

Table 3. Models for survival+movement of each age class in the Marys River network, assuming some connectivity between populations. S_x is as defined in Table 2, except $n_{(x)t}^{LOCATION}$ is the number (plus 1) of individuals estimated in Class x in year t at some LOCATION in the network. Note that the "survival" of Class 1 depends on local density of Class 1 in each stream, but the survival of older classes is usually linked to the density of those classes in other streams. This pattern is consistent with movement of older classes among streams. For example, although survival of Class 2 in MRBC is zero (no Class 3 fish have been observed there), Class 4 individuals are observed in this stream. The large positive intercept of regression for this model indicates that Class 3 fish move into MRBC after the Fall census, and the negative slope of regression for this model indicates that the survival of these immigrants depends on the density of Class 3 in the entire NETWORK. Because local survival or immigration/emigration of the more mobile classes can depend on class densities in multiple locations, we searched for effects of density in each location on local "survival" rates and selected the more explanatory models for each age class. Models shown are based on data gathered between 1994 and 1998, with the exception of the Class 5 model for MRBC. In this stream, Class 5 is observed infrequently, and no regression would have been possible without the 1999 data. Correlation coefficients are given for the models shown and for similar models based on all available data for each population. High R^2 for models based on both data sets (1994-98 vs. all years) indicates that all data are in agreement; however, we use the models shown because low sample sizes in 1993 and 1999 reduce our confidence in class size estimates for these years.

Population	Class	Survival+Movement model	SD_{resid}	P-value	$R^2_{94\text{-}98}$	$R^2_{All\ data}$
WMR	1	$S_1 = -0.0056\ n_1^{WMR} + 1.2799$	0.5056	0.061	**0.88**	0.87
	2	$S_2 = -0.0032\ n_2^{EMR} - 0.8557$	0.2803	0.076	**0.85**	0.92
	3	$S_3 = -0.0020\ n_3^{WMR} - 0.1139$	0.1611	0.111	**0.79**	0.79
	4	$S_4 = -0.0132\ n_4^{NETWORK} + 3.4043$	0.7261	0.099	**0.81**	0.64
	5	$S_5 = -0.9860$	2.2092	-	-	-
MRBC	1	$S_1 = -0.0033\ n_1^{MRBC+EMR} + 2.9078$	0.2031	0.011	**0.94**	0.95
	2	$S_2 = -4.6052\ (0)$	0	-	-	-
	3	$S_3 = -0.0029\ n_3^{NETWORK} + 5.2410$	0.1813	0.053	**0.90**	0.80
	4	$S_4 = -0.0239\ n_4^{NETWORK} + 3.1143$	1.8857	0.176	**0.67**	0.49
	5	$S_5 = -0.0238\ n_5^{NETWORK} + 2.4398$	0.2754	0.077	-	**0.99**
EMR	1	$S_1 = -0.0039\ n_1^{EMR} + 1.7409$	0.3397	0.043	**0.92**	0.86
	2	$S_2 = -0.0044\ n_2^{EMR+MRBC} + 1.8356$	0.7534	0.059	**0.89**	0.72
	3	$S_3 = -0.0186\ n_3^{NETWORK} + 5.2203$	1.0216	0.156	**0.94**	0.93
	4	$S_4 = -0.1198\ n_4^{EMR} + 4.2741$	0.1518	0.001	**0.99**	0.99
	5	$S_5 = -0.0166\ n_5^{NETWORK} + 1.4620$	0.4277	0.169	**0.93**	0.93

Table 4. Projected population risks under different models. The "**base model**" for each population is formed from the recruitment and survival models shown in Tables 1-3. The "**higher variance**" models increase the variance in recruitment, survival or both by multiplying the standard deviation of model residuals by a factor of 1.5. The "**truncated survival**" models do not allow survival >1, which reduces the potential for immigration (and interacts with observation/sampling error to cause conservative projections of population size). The "**higher flow**" models multiply stream flows by a factor of 2, which also increases the variance in flow. The "**lower flow**" models divide flows by 2, decreasing flow mean and variance. The "**lower capacity**" models simulate fewer spawning gravels and smaller habitats by reducing recruitment, increasing density-dependence, or both. Habitats are roughly halved in size by reducing the intercept of the recruitment model and/or doubling the (negative) slope of the density-dependent survival/movement models. The "**10% harvest**" models remove exactly 10% of Class 1 in each year when the class exceeds 500 individuals. ***Projected risk is the probability that the population will fall below 50 (including <20 adults) within a 100-year period***, estimated from 500 simulations per model. The range of risks shown for each population within the Marys River network derive from 32 model combinations applied to this network. When populations in WMR, MRBC and EMR are assumed to be isolated from the Marys River network (not shown), their risks rise significantly (see text). Note that all models predict the population or metapopulation in the Marys River is more robust than any other, despite the potential for frequent local extinction within each tributary.

Population	base model	higher recruit variance	higher survival variance	higher variance	truncated survival	higher flow	lower flow	lower recruit capacity	lower survival capacity	lower capacity	10% harvest
Gance	0	0	.01	.05	0	0	0	**.17**	.05	**.49**	0
Frazier	.01	.02	.01	.03	.01	**.99**	0	1	.01	1	.01
Foreman	.02	.04	**.29**	**.38**	.07	.02	.02	.01	**.54**	**.14**	.03
Marys River *pooled*	0	0	0	0	0	0	0	0	0	0	0
Marys River *networked*	0	0	0	0	0 - .02	0	0	0	0	0	0
WMR	0 - 1	0 - 1	.01 - 1	.03 - 1	1	0 - 1	0 - 1	.01 - 1	**.53 - 1**	**.25 - 1**	0 - 1
MRBC	0 - .06	0 - .06	0 - **.10**	0 - **.11**	**1**	0 - **.36**	0 - .03	0 - 1	0 - **.36**	0 - 1	0 - .03
EMR	0 - .04	.01 - **.14**	0 - .09	.01 - **.31**	0 - **.53**	0 - .07	0 - .06	0 - .03	.07 - **.26**	.01 - **.24**	0 - .05

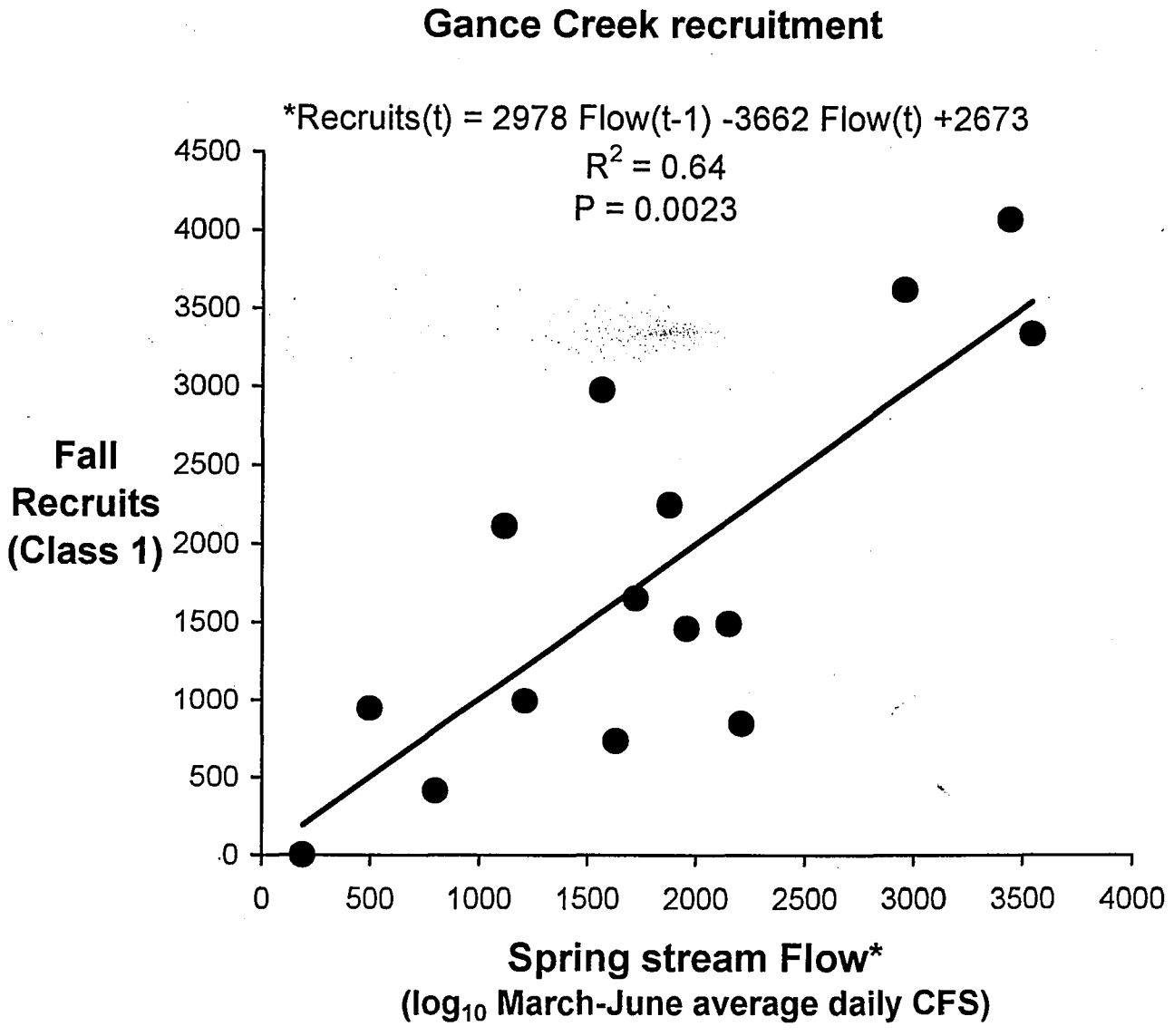

Fig. 1. Daily stream discharge during the "Spring" months (March-June) predicts recruitment in Gance Creek. Recruitment of age 1+ individuals in year t is positively related to Spring flows in year t-1 (when recruits were in the egg stage) and negatively related to Spring flows in year t (when recruits were very small). Including the number of repreductive adults in the model actually decreases the fit, because adults explain none of the variance and two data points are lost (age 1+ recruits in year t must be regressed on adults in year t-1, and there is a break in the data between 1985 and 1993).

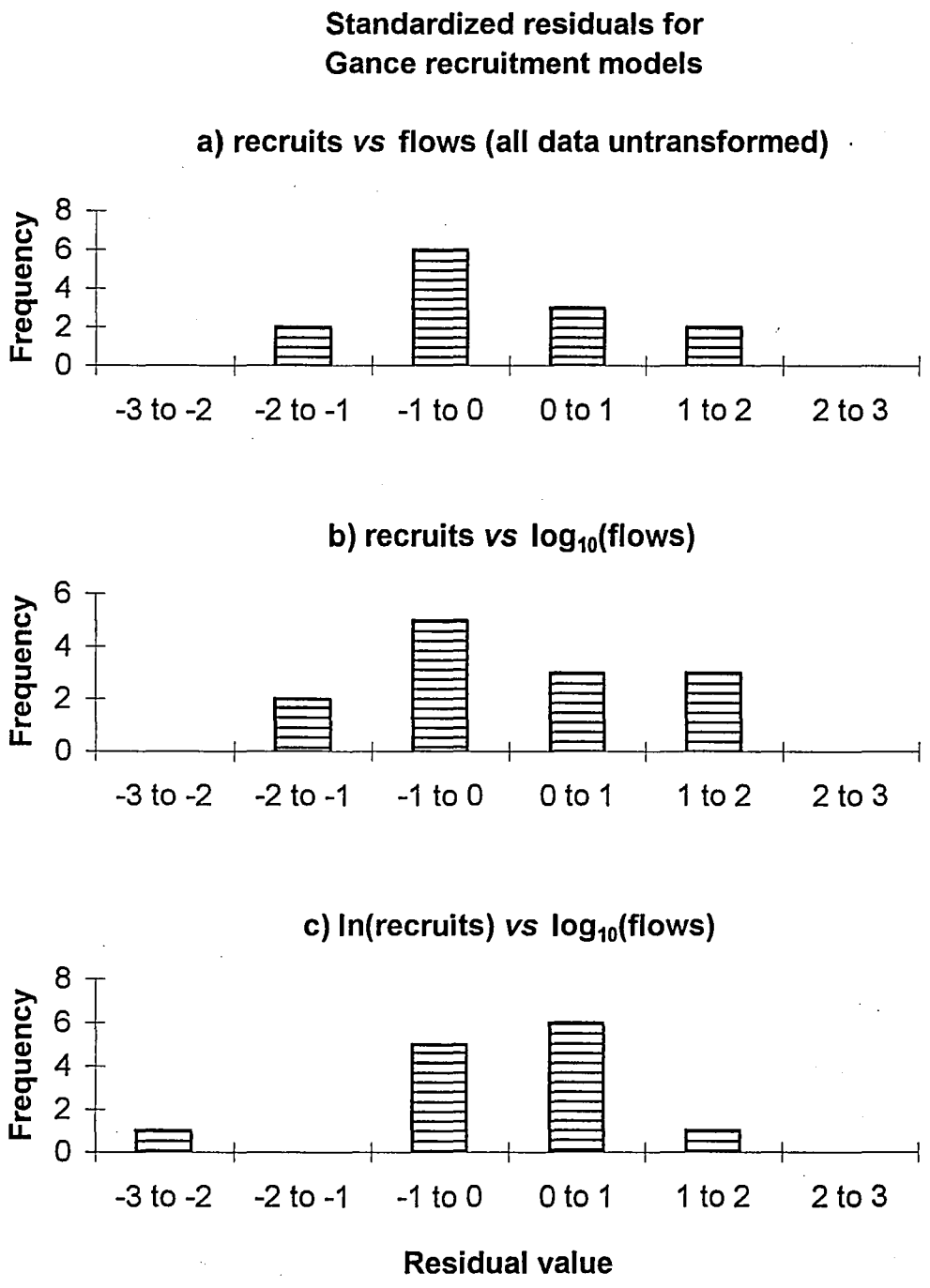

Fig. 2. Standardized residuals from regressions of recruitment on stream flow, using three different transformations for recruitment and flow data from Gance Creek. We use untransformed recruitment data and $\log_{10}$-transformed flow data (b) to construct all recruitment models (Table 1). For survival models (Tables 2 and 3), we use ln-transformed survival data and untransformed class density data to normalize residuals. Our simulations then sample from a normal distribution of residuals to model the unexplained variance in recruitment and survival.

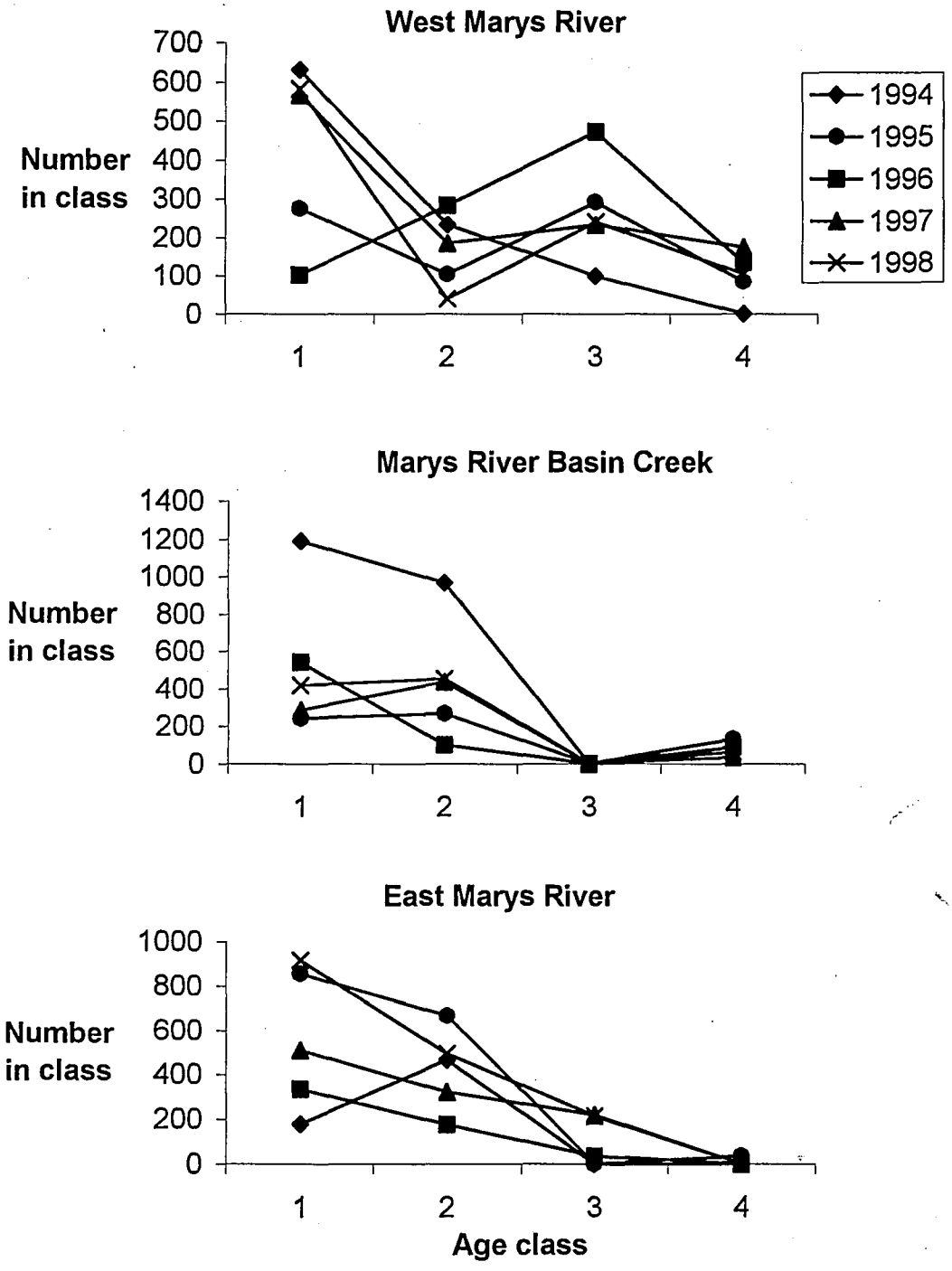

Fig. 3. Evidence for movement among tributaries of the Marys River. An excess of Class 3 in WMR corresponds with a deficit (0) of Class 3 in MRBC. This pattern is consistent with movement of Class 3 fish into WMR and movement of Class 4 fish into MRBC. Sampling error is not likely to cause this consistent pattern, because sampling error should vary among years and streams.

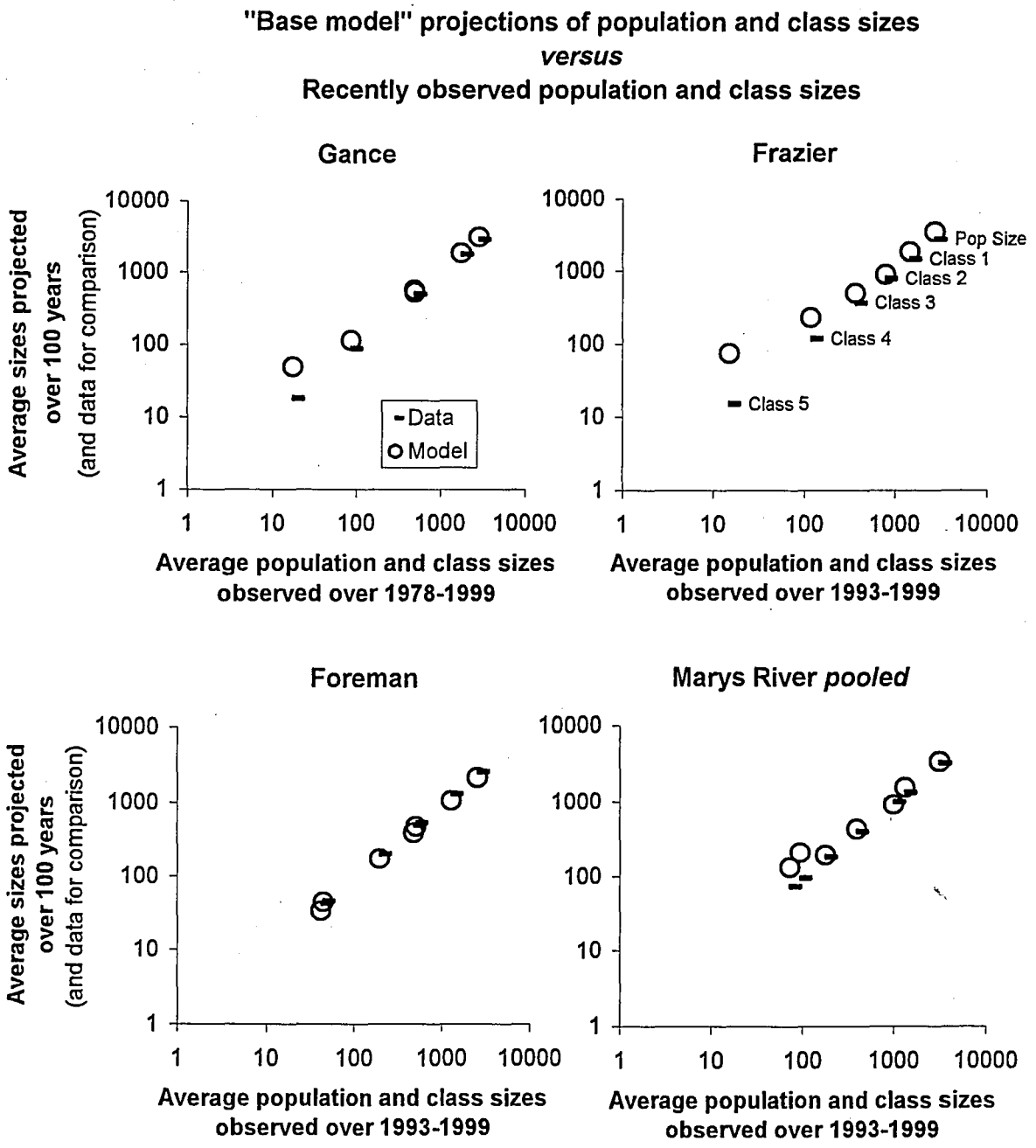

Fig. 4. Population projections, using the recruitment and survival models shown in Tables 1 and 2. Projected class and population sizes (circles) differ little from recently observed sizes (dashes), indicating that no trends in size are expected if environmental conditions do not change. The slight increase in older class sizes predicted by the Gance, Frazier and Marys River *pooled* models may be an artifact of the large standard deviation in survival of these classes (see Table 2), combined with our assumption of normal residuals. This artifact would not be critical to the results of our comparative study, because we use similar models for isolated and networked populations and because recruitment is not sensitive to the number of surviving adults.

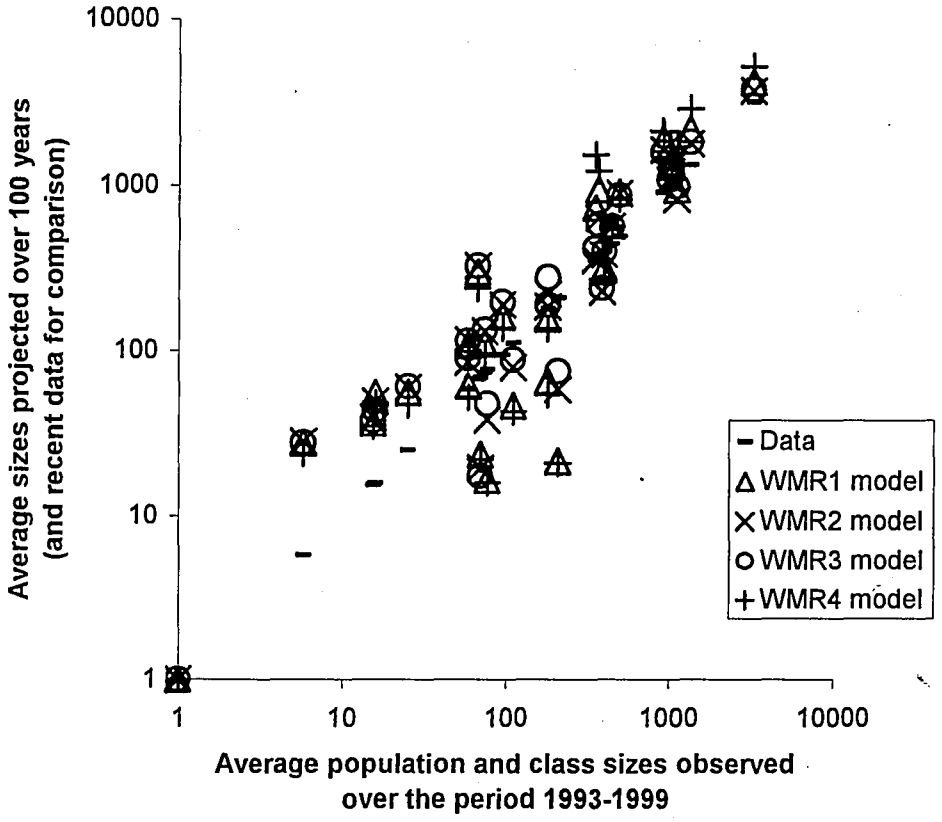

Fig. 5. Projections of population and class sizes in the Marys River network under four different recruitment models. There are several potential recruitment models for each local population in the network (see Table 1), allowing 32 model combinations. All combinations were simulated, with minimal deviation in results between models. Over 70% of the small variance in results was explained by the WMR recruitment model. This graph shows four models, each based on MRBC recruitment model 3 and EMR recruitment model 1, and each using a different WMR recruitment model. All 32 network models predict that future Marys River population and class sizes will be similar to those currently observed, assuming environmental conditions remain unchanged.